PSYCHE

THE REPRODUCTIVE PATTERN OF
DINOPONERA GRANDIS ROGER
(HYMENOPTERA, PONERINAE)
WITH NOTES ON THE ETHOLOGY OF THE SPECIES

By Caryl P. Haskins[1] and Paul A. Zahl[2]

Introduction

The recent stimulating suggestions of Hamilton (1964*a*; 1964*b*; 1970) that social behavior in the Hymenoptera may have evolved at least in part as a consequence of particular conditions favoring kinship selection offered by the haplodiploid pattern of sex deter- mination in the higher Hymenoptera have, among other things, given special significance to the detailed study of breeding patterns in social members of that order. In this connection, we have for several years been investigating the breeding patterns, the effects of excessive inbreeding, and the modes of formation of new colonies, in a number of primitive ants. In this context, species in which either sex lacks functional wings at maturity take on special interest. Outside the Dorylinae and scattered groups of socially parasitic ants in other subfamilies, such forms, in which a typical mating-cum- dispersion flight is evidently impossible, are rather rare among the higher Formicidae. It is notable, however, and may be of a yet unidentified evolutionary significance, that marked brachyptery and even aptery in females are unusually evident in the two most generalized subfamilies of ants, the Myrmeciinae and the Ponerinae. Within the single genus *Myrmecia,* for example, forms in which the reproductive and colony-founding female is subapterous or even wingless and exhibits radically reduced thoracic musculature are by no means uncommon. Among the Ponerinae, as Wheeler pointed out some years ago (1933), wingless eratogynes replace the normal female forms in several genera, such as *Acanthostichus, Eusphinctus, Megaponera, Onychomyrmex,* and *Pletroctena.* These ergatogynes,

[1]Carnegie Institution of Washington, Washington, D. C.
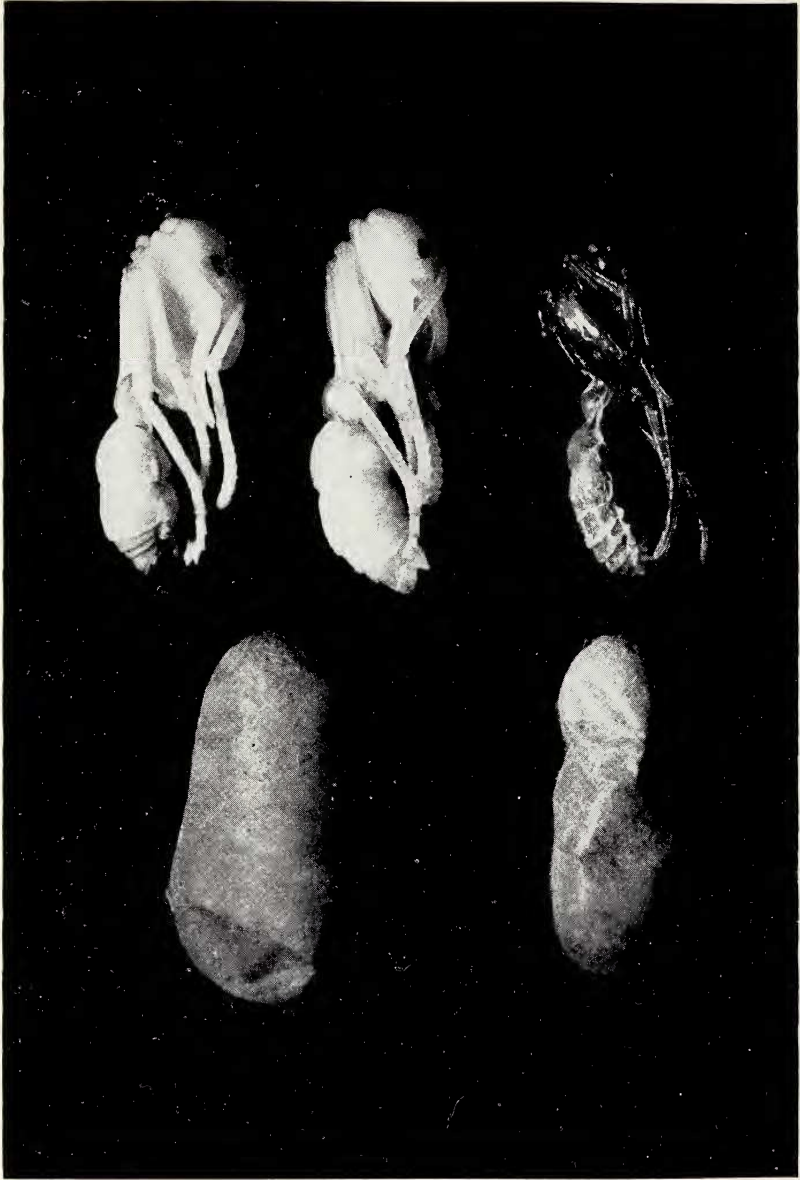[2]National Geographic Society, Washington, D. C.

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Figure 1. Worker cocoon and pupae (upper), male cocoon and pupa (lower) *Dinoponera grandis*, reared respectively in colony fragments A and B, described (× 2).

to be sure, are still morphologically distinguishable from the workers. In *Leptogenys, sens. str.,* however, in some species of *Rhytidoponera,* and in *Diacamma, Streblognathus,* and *Dinoponera,* no caste morphologically distinguishable from the worker has ever been reported, though normal males, in some cases evidently well adapted to secure outbreeding within the species, are the rule. A number of years ago Wheeler and Chapman (1922) described a male of a Philippine species of *Diacamma in copula* with an individual morphologically indistinguishable from a typical worker, suggesting the lack even of an identifiable ergatogyne in this species, the "workers" differing only in the presence or absence of a functional spermatheca and perhaps in the degree of ovariole development — a situation well known in several species of *Rhytidoponera* (Haskins and Whelden, 1965). It became of interest, therefore, to learn whether such workerlike individuals form the normal reproductive caste in *Dinoponera.* That this situation, if real, could typify a rather ancient evolutionary condition is hinted by earlier findings of F. M. Carpenter. Carpenter suggested some years ago (1930) that a fairly close fossil relative of both *Dinoponera* and *Streblognathus* may be *Archiponera wheeleri,* described by him in 1930 from the Miocene Florissant shales of Colorado. The absence of described morphologically differentiable females in either *Dinoponera* or *Streblognathus* (1929; 1930) gave special emphasis to a search for such a caste among the fossils of *Archiponera.* No examples were discovered, though typical winged males were described.

The observations to be presented confirm the production of workers by one or more wild-collected females of *Dinoponera grandis,* indistinguishable from workers in external morphology, in the artificial nest.

Material

The monotypic ponerine genus *Dinoponera* has been known since 1830, when its single species, *D. grandis* was described by Guérin from Pará and Bahia, Brazil (1830). Carpenter noted (1930) that apparent morphological affinities of both it and the South African monotypic form *Streblognathus aethiopicus* to fossils of the Miocene *Archiponera wheeleri* in the Florissant shales could suggest that the two modern species are ancient relicts of an archaic ponerine complex which originally had a much wider distribution.

The range of *D. grandis* given by Carlos Emery (1911) is "Middle American tropics as far as Paraguay," and collecting localities for various described subspecies recorded up to that time

include São Paulo, Missiones, Espiritu Santo, Matto Grosso, Bahia, and Pará in Brazil, as well as "Pérou." For the present study, the authors selected a single, restricted population of the typical form, not far from Pará, which they have intermittently had under independent field observation since 1937. Some 30 "workers," together with more than a dozen cocoons and larvae, were taken from a typical colony by one of us (PAZ) in December, 1969, and brought to Washington, D. C., where they were housed in observation nests and the recorded observations made over a period of somewhat more than a year.[3]

Methods and Observations

The colony was approximately evenly divided, and the fractions housed in glass-and-plastic earth-containing Lubbock nests, 45.7 cm × 28.5 cm, and 3.0 cm in depth. Two of these were stacked in each of 2 aquaria of dimensions 61 cm × 29.0 cm × 22.5 cm, to serve as foraging arenas. These aquaria were covered at all times with 2 glass plates, with an aperture of 1.0 cm, through which was inserted the stem of a Weston Mirroband recording thermometer. Room temperature was kept constant at 75° F. Since the entrances to the Lubbock nests were kept open at all times, and soil was excavated and carried into the arena fairly continually by the ants, humidity usually approached saturation.

A. Breeding Pattern

The eggs of *D. grandis* are comparatively large (approximately 2.5 mm in length) and unusually elongate. They cohere in packets, usually of approximately 6 to 15 ova, and are assiduously tended by the workers. Indeed, the nurses spend much time in the nest at rest with such packets held in the mandibles. Shortly before hatching, single eggs are detached from the packet, licked and tended individually, and commonly deposited separately on the nest floor. Immediately after hatching the larvae are separately attended and frequently carried about. We believe (though it is not yet proved) that for the first, and possibly the second, instar they are fed ingluvially by the nurses. Older larvae are given partially dissected arthropod prey in typical ponerine fashion, the fresh prey being commonly deposited on the ventral surface. The larvae develop rapidly through this stage. When about to spin, they are temporarily covered with earth in the typical ponerine manner. The cocoons of
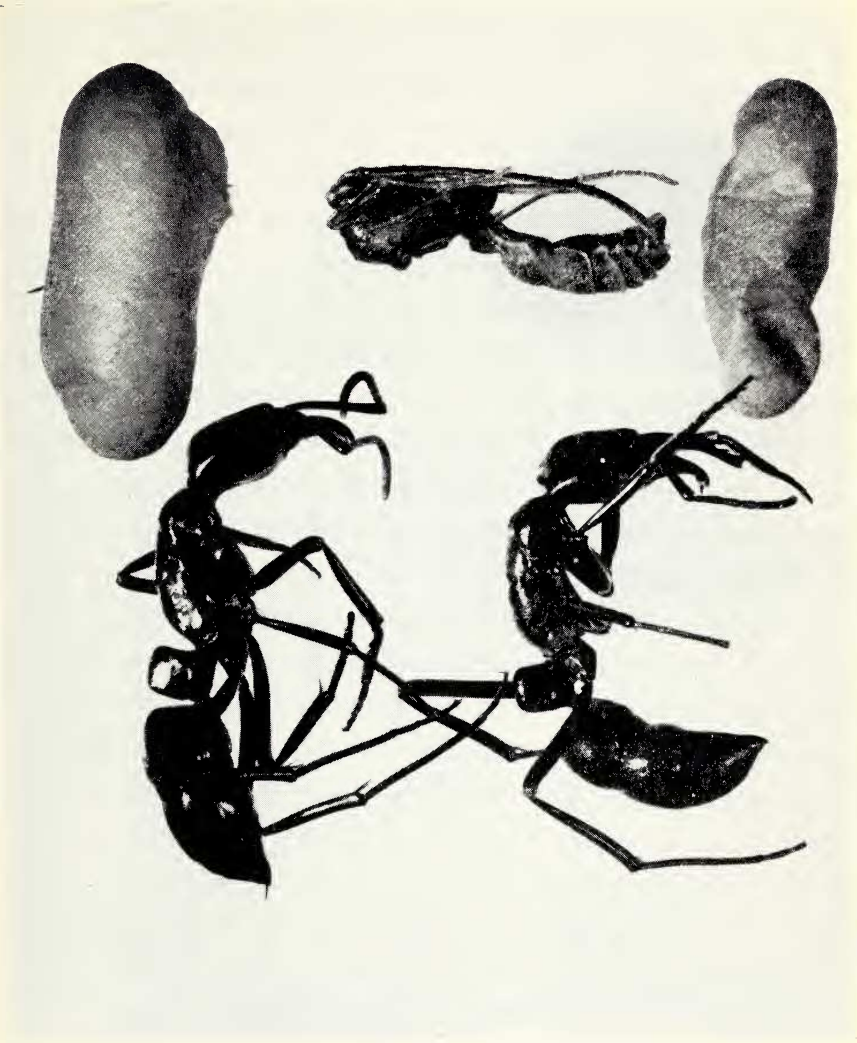
Figure 2. Workers (left) ; worker cocoon ; male pupa ; male cocoon *Dinoponera grandis* ($\times$ 2).

Table 1

Records of Brood Rearing in Colony Group A

Date	Brood and Description
12/6/69	First egg seen.
2/7/70	Two half grown larvae; 7 small larvae.
2/15/70	Two large larvae; 5-7 small larvae; about 6 eggs.
2/27/70	Four large larvae; 5 medium larvae; 4 small larvae; eggs.
3/3/70	Four large larvae; 4 medium larvae; eggs.
3/18/70	Two cocoons; 4 large larvae; numerous medium-small larvae.
3/20/70	Three cocoons; 4 large larvae; 1 small larva.
6/11/70	Three cocoons; 3 medium larvae; eggs. Two cocoons opened. One contained a young, unpigmented, normal worker pupa, the second a semipupa.
7/15/70	A further cocoon opened, revealing a partially pigmented, normal worker pupa.
8/28/70	Three cocoons; 0 larvae; packet of about 10 eggs.
9/4/70	First larva in new group hatched.
9/16/70	Two additional larvae hatched.
9/20/70	Fourth and fifth larvae hatched.
9/25/70	Remaining pupa in cocoon died and extracted by workers. Nearly mature, normal worker pupa.
10/8/70	First new cocoon spun. Two large larvae; 2 medium larvae; eggs.
10/10/70	Second larva buried for spinning.
10/11/70	Second cocoon spun.
10/12/70	Meconium appeared in first cocoon.
10/14/70	Meconium appeared in second cocoon.
10/15/70	Third cocoon spun.
11/3/70	Fourth larva buried for spinning. (The nest was inadvertently disturbed a few hours later. This larva was then prematurely disinterred by the workers and perished.)
11/29/70	First cocoon hatched, eclosing nearly pigmented, normal young worker. Pupa in a second cocoon died and was extracted. A nearly mature worker.
12/10/70	First larva hatched from new egg group.
12/29/70	One large larva; 1 medium; 1 small.
12/30/70	New larva hatched (1 large; 1 medium; 1 small).
1/2/71	One large larva; 2 medium; 1 small.
1/6/71	First larva banked for spinning (A.M.).
1/6/71	First cocoon spun (P.M.).
1/7/71	Fifth larva hatched.
1/9/71	Sixth larva hatched.
1/10/71	Meconium in first cocoon.
1/13/71	Seventh larva hatched (1 cocoon; 2 medium, 4 small larvae).
1/27/71	Second larva banked for spinning (P.M.).
1/28/71	Second cocoon spun (2 large, 3 medium, 1 small larva; no eggs).
2/2/71	Meconium in second cocoon. First new egg.
2/4/71	Third larva banked for spinning. Second egg.
2/5/71	Third cocoon spun.

2/8/71   One cocoon destroyed by nurses. Pupa not recovered. (Two
           (Two cocoons; 3 large larvae.)
2/10/71   Fourth larva banked for spinning.
2/11/71   Fourth cocoon spun (3 cocoons; 2 large larvae).
2/16/71   Fifth larva banked for spinning.
2/17/71   Fifth cocoon spun (4 cocoons; 1 large larva; no eggs).
2/21/71   Sixth larva banked for spinning.
2/22/71   Sixth cocoon spun (5 cocoons; 1 egg).
2/25/71   Second cocoon rejected from nest. Opened, disclosing normal,
           apparently healthy worker pupa, entirely unpigmented. (Four
           cocoons, eggs.)
3/6/71   Third cocoon rejected from nest. Opened, disclosing perfect, ap-
           parently vital worker pupa, with eyes fully pigmented.
3/14/71   Fourth cocoon rejected from nest. Opened, disclosing perfect,
           apparently vital worker pupa, eyes fully pigmented, and body
           pigmentation well advanced.
3/19/71   Fifth cocoon rejected from nest. Opened, disclosing perfect
           worker, with eyes fully pigmented, and body pigmentation
           well advanced.
4/13/71-   Sixth cocoon hatched, eclosing perfect worker of adult pigmen-
4/14/71   tation.

workers are large and robust (approximately 23.0 mm $\times$ 8.5 mm)
and formed of a tough, dark brown silk. In eclosions of the imago
that we have witnessed, attendant workers have assisted in opening
the cocoon at the anterior pole, but it is possible that isolated pupae
can emerge unassisted, as in some other Ponerinae. In the artificial
nest, young workers have been almost fully pigmented at eclosion.
It is likely that this is also the case under natural conditions, a situa-
tion typical of some other members of the Tribe Ponerini.

The two fragments of the collected colony were kept separate
throughout the observations, and separate records of brood rearing
were maintained. That for Group A is indicated in Table I.

Thus from brood of this group, originally comprising 10 wild-
collected "workers," 15 cocoons of worker size and form were
matured. The contents of 11 were definitely identified as worker
pupae or adults. In the remaining 4 the cocoons were workerlike
in form, but the contents could not be verified because of their
early death or premature examination. The developmental periods
recorded for 8 larvae followed from hatching to cocoon spinning
were 24, 25, 27, 29, 31, 43, 44, and 44 days. The interval between
the covering of a spinning larva with soil and the cleaning of the
completed cocoon was 1 day for each of 6 individuals. The interval
between the completion of the cocoon and the appearance of the
meconial spot in 4 individuals was 4, 3, 4, and 5 days. Periods

recorded from cocoon spinning to pupal maturity for 2 individuals were respectively 50-51 and 52 days. As suggested by the data of Table 1, some ecological deficiency (perhaps too low a temperature) may have been responsible for the premature abandonment of all but 2 of the cocoons by the nurses, and may have prolonged times to eclosion abnormally in those that hatched.

It was clearly evident that at least 1 adult fertile brood female, morphologically indistinguishable from a worker but capable of producing female progeny, had been included in the original wild collection

The history of brood production in the second group of workers was quite different. Here, despite intensive care, egg production was poor, and the brood total low Only 2 cocoons were produced, both of male size and form (at about 20.0 mm × 6.0 mm, fairly reliably distinguishable by inspection from those of workers). One of these was opened artificially, disclosing a nearly mature male pupa. The second eclosed naturally, revealing a perfect male. No worker brood was produced. It thus appears that a fertilized ergatogyne was lacking in the second fraction of the colony

B. Mating Pattern

In *Dinoponera,* as in *Streblognathus* and *Archponera,* the males are decidedly smaller than the workers (see Figures 1, 2, and 3). They are much more lightly pigmented at maturity, and are relatively fragile. The compound eyes are large and the ocelli unusually prominent, conspicuously reflecting low incident light. The wings are well developed, and adults once emerged from the nest fly actively. Within the parent colony, however, they are surprisingly inert. At least until full maturity they assume the pupal posture when disturbed and are carried by the workers as though they were brood, as the authors have frequently observed both under natural conditions and in the artificial nest. In the latter situation, males are often held in the mandibles of immobile workers as though they were brood, even when the colony is slightly stimulated. The males may well be night fliers of somewhat restricted range. We have not yet witnessed mating flights under natural conditions, nor determined the precise mode of formation of new colonies.

Note on the Ethology of D. grandis

Ever since Henry Walter Bates (1892) almost eighty years ago described columns of *D. grandis* "marching through jungle thickts" the implication has been widely assumed and reiterated that the
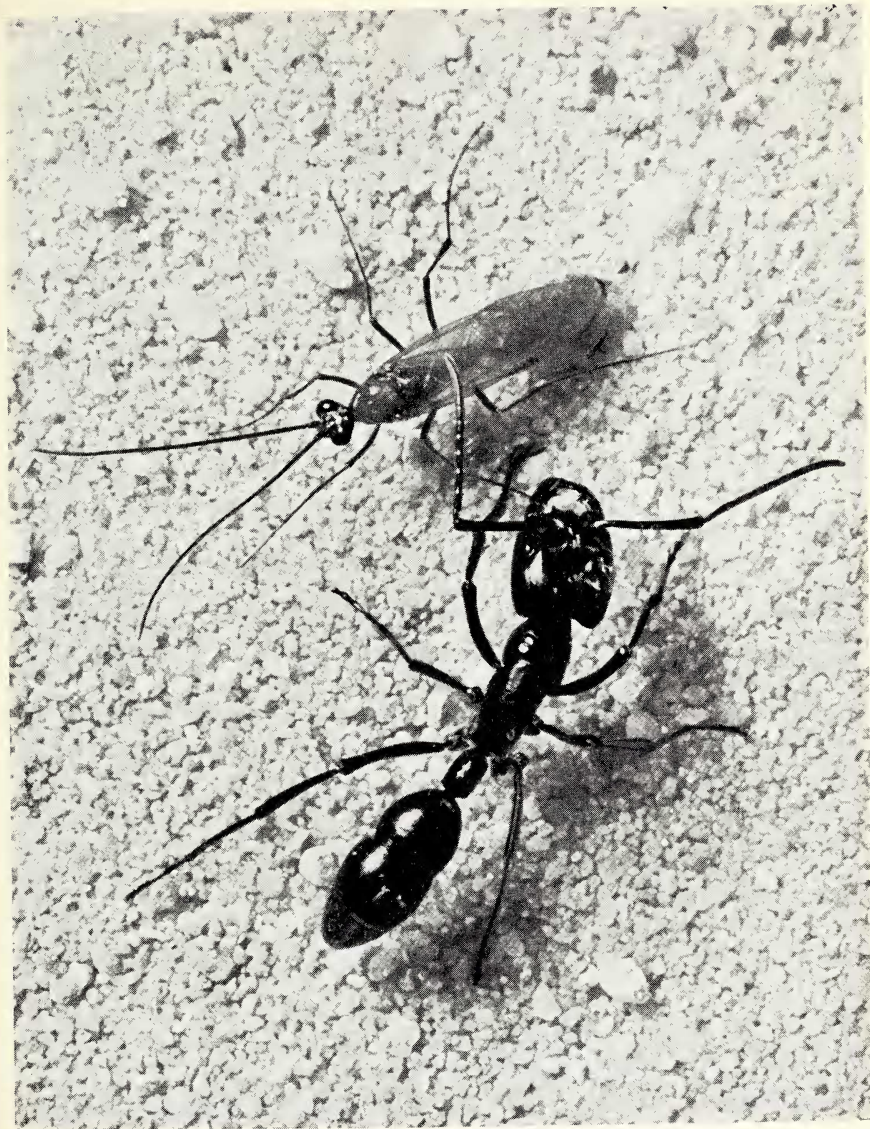
Figure 3. Worker (left) ; male (right) of *Dinoponera grandis*, showing disparity in size ($\times$ 2).

species is a typical column termite-raider, foraging in the general pattern of *Termitopone* in the New World or *Megaponera* in the Old. This conception has most recently been alluded to by Sudd (1967). All our observations, however, including those made both in the artificial nest and under natural conditions, seem contrary to this. Foraging workers of *Dinoponera* may indeed follow one another in tenuous, ill-defined columns. But all those that we have observed under natural conditions have been extremely loose formations — so diffuse as hardly to merit the name. Moreover, we have never seen termite raiding under natural conditions. In the artificial nest, the species proved a general and uncritical feeder on a wide range of arthropod prey, including the larvae and pupae of other ants when offered. Workers of *Termes flavipes,* when presented in debris outside the nest, were indeed sought out, captured, and carried in: but with no detectably greater readiness than other insect prey. If *Dinoponera* is specialized to termite feeding at all, it is to a very slight degree. As with other members of the Ponerini, sugary substances are readily accepted — and, indeed, probably required — by the adults.

Summary

The failure to discover a morphologically distinct female caste among members of the archaic ponerine genera *Dinoponera* or *Streblognathus,* or in the fossil genus *Archiponera,* has long led to the suspicion that, as in *Diacamma* and species of *Leptogenys* and *Rhytidoponera,* such a caste may in fact be lacking and may be replaced by a reproductive form morphologically very similar if not identical to the worker but physiologically and structurally capable of fertilization and the production of worker brood. This suspicion has now been experimentally verified in *Dinoponera grandis* in the artificial nest.

Notes are appended on certain features of the breeding pattern and ethology of the species.

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